THE PLEISTOCENE RACES OF CERTAIN BRITISH INSECTS AND DISTRIBUTIONAL OVERLAPPING.

By J. W. Heslop Harrison, D.Sc., F.R.S.

In 1916 I published a comprehensive series of papers (*Naturalist*, 1916, pp. 163-166; 194-198; 273-278; 358-362; 377-382) under the general title "The Geographical Distribution of the Subfamily Bistoninae" in which the whole of the world species of the group were reviewed. In that work, the view was advanced for the first time that many British species of Lepidoptera, of which *Nyssia zonaria*, Dup., affords a good example, had survived the vicissitudes of the Great Ice Age on Lands, long since overwhelmed by the waves, lying to the west of the present shores of Ireland and the Outer Hebrides. From those havens of refuge, it was suggested that, as the climate ameliorated at the close of the Glacial Period, and the ice sheets waned, such forms pressed to the west and south to recolonize areas set free of ice.

Later (*Trans. Nat. Soc. Northl. Durh. and Newcastle-upon-Tyne N.S.*, Vol. 6, 1924), a second paper* appeared from the pens of Mr Wm. Carter and myself which extended the same idea to cover the distributional and other problems presented by the British races of the butterfly *Aricia agestis*, Hb. (=*A. medon*, Esp.). At the same time, it was demonstrated that the Durham and Northumberland habitats of the species constituted a zone of hybridization in which ordinary southern *medon* (*agestis*) overlapped and interbred with the Scottish subspecies *artaxerxes*, Fab. It was likewise established that, as a result of this interbreeding, there had come into being a mixed population comprised of individuals exhibiting all the characteristics of one or other of the parent subspecies, intermingled with others displaying every possible recombination of those characteristics. A further point made was that the position was complicated to a remarkable extent by the presence of aberrant insects owing their genesis to genetic interactions of various types.

Included in the hybrid population, as was clearly indicated, were forms alleged by many to represent a distinct race, intermediate to *agestis* and *artaxerxes*, to which Stephens, quite arbitrarily, applied the name *salmacis*—a procedure wholly indefensible.

Further, the thesis was developed that *artaxerxes* itself had evolved in isolation from a contingent of *A. agestis*, cut off during the Glacial Period by an ice barrier from the main stocks of the species. In accordance with the then accepted opinion that *agestis* still existed in Ireland, these refugia were placed in ice free areas lying beyond the present-day coasts of that country. Now that the claims of the species to a place in Irish faunal lists have been rejected, we are compelled to look to the West of Scotland, or to the Scottish Western Isles, for the required refuges. Moreover, whilst it cannot be denied that Tertiary relict forms, exemplified by the moss *Myurium Hebridarum*, Schimp., have persisted throughout the whole of the Glacial Period, it seems almost certain that the history of all the British species studied in the papers discussed can only be dated back to the last Interglacial Period, or even

*The contents of this paper are summarized by Ford in his "Butterflies" (pp. 296-298, p. 314), but no reference to the original work is supplied.

to some period of temporary retrogression during the last Pleistocene glaciation.

Let us now consider the possibility that it is to the Western Scottish areas to which we have to look for ice-free refuges in which *artaxerxes* evolved. Clearly, if these were able to maintain colonies of *A. agestis* during the last Pleistocene glaciation, they must have supported its food plant, *Helianthemum vulgare*, Gaertn. That being so, if one has to base a judgment on the present status of the plant in the West of Scotland, the whole of the Hebrides, Inner and Outer, must be excluded, for only on Lismore of all the Western Isles does rockrose grow. Attaching due weight to the glacial phenomena observable on Lismore, and to its geographical position, it seems very unlikely that it provided the necessary refugia. However, when we realize that rockrose flourishes elsewhere in v.-c. 98, and that other obvious Interglacial survivors like *Zygaena purpuralis*, L., and *Z. achilleae*, Esp., may still be captured in the Oban area, it appears quite possible that sheltered ice-free areas existed in Argyllshire in which *agestis* persisted, and gave rise to the subspecies *artaxerxes*.

Again, in spite of the fact that, taking only the present range of the rockrose into account, the Inner and Outer Hebrides cannot be brought in the discussion, the plant may not have been absent from the islands during the final Interglacial Period. Toward its closing stages, high land levels, marking isostatic adjustments resulting from the removal of the ice load, supervened. Almost certainly, the islands of the Rhum, Eigg, Canna and Muck series would constitute, with the adjoining mainland, one continuous stretch of land. This would entail exposure of the limestone formations now just under the sea on the southern approaches to Muck. Besides, the now rapidly weathering limestone areas of the Monadh Dubh, Rhum, must at that period have been much more extensive. In addition, whilst preferring limestone, rockrose does not reject basalts of which Rhum, Eigg and Canna provide an abundance. Since Rhum was, for the most part, free from ice during the last Pleistocene glaciation, the chance that rockrose, with the insect, survived in the Small Isles area cannot be disregarded. That the islands remained isolated long enough for widely divergent forms to evolve must be granted, as endemic species like the eyebrights, *Euphrasia Heslop-Harrisonii*, Pugsl., and *E. rhumica*, Pugsl., as well as the strange endemic orchid related to *Orchis ericetorum*, Linton, prove so decisively. This would imply that, whilst eustatic rises in sea level at the close of the Ice Age once more cut off the islands from the mainland, as the late glacial raised beaches demonstrate, later the insect, during a period of renewed land connections, again isostatic in origin, was able to pass to the mainland.

At this stage two points need emphasis; it is quite possible, although not likely, if due weight is attached to the fact that *artaxerxes* never leaves rockrose, that the other food plants of typical *agestis*, various species of *Erodium*, should be taken into consideration. Secondly, since an Irish relict colony of rockrose has been discovered, Ireland may still have provided the species with its refugium.

For a long period I regarded *Aricia agestis* as unique in providing an example of overlapping and interbreeding races in Britain. Now, as the outcome of protracted studies of Hebridean insect faunas, I re-

cognize that the species furnishes only one of the many instances available, not only in the Lepidoptera, but also in other insect orders. Amongst the Lepidoptera, *Polyommatus icarus*, Rott., with its race *clara*, Tutt; *Maniola jurtina*, L., with *splendida*, B. White; *Argynnis aglaia* with *scotica*, Watk.; *Eupithecia pulchellata*, Stph., with *hebudium*, Sheld.; *Coenonympha tullia*, Mull., with its two subspecies; *Euphyia bilineata*, L., with *atlantica*, Staud.; *Thera cognata*, Thnb., with its island race, and the Protean *Triphaena comes*, Hb., supply an excellent group of examples. In particular, I have already shown (*Vasculum*, xxx, p. 58, 1945) that the case of the common blue butterfly, *Polyommatus icarus* with its race *clara*, Tutt, runs exactly parallel with that of *A. agestis*. On the Durham coast, forms precisely the same as those captured in the Outer Hebrides fly alongside every type of intergrade between *clara* and the type. Indeed, so extreme are some of the Durham females, that this summer I was quite unable to differentiate a series caged up for eggs from a similar lot from the Isle of Barra. Also in harmony with the *agestis* position, in inland areas in Northumberland and Durham the ordinary English insect, with some intergrades, dominates the colonies.

Of the other species mentioned, the influence of the Scottish Interglacial races of *Argynnis aglaia* and *Euphyia bilineata* is also felt as far south as the North of England. On the other hand, the zones of hybridization involving *M. jurtina*, *T. cognata* and *E. pulchellata* with their Hebridean races are restricted in some instances to the Inner Hebrides, and in the others to the same islands and the adjacent areas of the mainland. In the case of *Triphaena comes*, intergrading masked by dominance, epistasis and other phenomena depending upon segregation and recombination, occurs in the Hebrides, and north of a line from the Clyde to Angus, although light infiltration south of this line may be encountered.

In all of these instances, the weight of the evidence brings strong support to the opinion that these Scottish Interglacial races are correctly described as Hebridean, inasmuch as they have originated in ice-free Hebridean areas cut off during the last Pleistocene glaciation when the mainland was still enveloped in an icy covering.

Conspicuous amongst the representatives of other insect orders possessing a glacial history closely resembling that of *Polyommatus icarus* stands the Hymenopteron *Bombus smithianus*, White. This humble bee, whilst found on other fringing islands in the British area providing glacial relict stations, reaches its maximum population density in the Outer Hebrides, and in certain members of the Inner Group. In these islands it forms a very striking element of the insect fauna. As far as the Outer Isles are involved, it may be observed in every island, great and small, from Lewis to Barra Head. In the Inner Isles, it forms a permanent inhabitant of the Isles of Coll, Tiree, Gunna, Rhum, Eigg, Canna, Muck and Hyskeir. In addition, it has occurred sporadically on Raasay, South Rona and Scalpay. Although close search has been made for it, it has never been detected in Mull, Skye and Soay.

Most workers, including myself, rank *B. smithianus* as a distinct species; others, however, are inclined to regard it as a subspecies of *B. muscorum*, L. In any case, it has been evolved from *B. muscorum* at some date, geologically speaking, comparatively recent, and with that

species it clashes in the Rhum and Raasay groups of islands. On Rhum, Cann and Eigg, *B. smithianus* occurs in preponderating numbers whilst on Raasay its occurrence is sporadic, and *B. muscorum abounds.* Further, it should be emphasized that on all these islands a third related species, *B. agrorum*, L., flies also. In the Isle of Rhum, where the problem has been studied most closely, the ranges of *B. smithianus* and *B. agrorum* tend to remain distinct. Very different are the relations between *B. smithianus* and *B. muscorum*; whilst pure *B. muscorum* occurs but rarely, intergrades, generally, but not always, approaching *B. smithianus* are of frequent occurrence. On Eigg and Canna the same holds true. On the other hand, in Raasay at the Point of Eyre, insects forming a complete transition from *B. smithianus* to *B. muscorum* have been taken on several occasions. Obviously, in the zones of overlap, interbreeding has taken place ending in the evolution of hybrid populations of varying degrees of complexity.

Once more the explanation of these mixed populations lies in the fact that in *B. smithianus* we are dealing with a glacial "overwinterer" which has emerged from its Hebridean retreats to make contact with and interbreed with contingents of *B. muscorum* advancing northward and westward in the rear of the retreating ice. Nevertheless, as far as Raasay is concerned, the warning must be given that the postulated movement of *B. smithianus* may be quite recent; indeed, in my opinion, one irruption of that species took place during the last decade. On the contrary, it seems certain that, on Rhum, Eigg and Canna, the clash took place so long ago as Boreal times when Rhum and its neighbours received their quotas of southern plants and animals from mainland sources.

Of the other groups, the Odonata include at least one species on which the same type of phenomena is apparent; this is *Sympetrum striolatum*, Charp., and its race *nigrofemur*, Selys. Throughout the Hebrides, and more especially in the islands containing *Bombus smithianus*, the race *nigrofemur* swarms. In fact, this season (1947) it has hawked over the lochs, and far away from them, in prodigious quantities.

Even on the Scottish mainland, and in England as far south as Co. Durham, the blacklegged form may be found. However, it is noteworthy that, in Northumberland and Durham at least, intermediates crop up. Thus, once again, the phenomena made familiar by *Aricia agestis* and its subspecies *artaxerxes* have been repeated. In other words, it is clear that, in the race *nigrofemur*, we have a western Interglacial race, interbreeding in a zone of overlap with a second subspecies of southern proclivities. It deserves mention, too, that in the west the Welsh counties produce intergrades. This occurrence is just what one would anticipate from the superior mobility of such far-wandering forms as the different *Sympetrum* species.

The Hemiptera-Homoptera and Coleoptera likewise yield examples of the same type of behaviour although in these orders the necessary observational and breeding work with selected species are only in the initial stages. Amongst the Homoptera the Psyllid *Livia juncorum*, Latr., has been chosen, and as far as the work has gone, it appears clear that a dark Hebridean race exists which overlaps with the ordinary mainland form to give rise to intergrading forms on Gunna, Tiree and

Coll, and doubtless elsewhere. Much the same seems to apply to *Psylla dudai*, Sulc., and amongst the Coccids to *Chionaspis salicis*, L.

In the Coleoptera the two forms subjected to study are *Coccinella 11-punctata*, L., with its race *boreolitoralis*, Donis., and *Carabus problematicus*, Hbst. The first named insect, when bred in numbers from the Rhum sand dunes, produced forms intermediate between the extreme *boreolitoralis* and the ordinary form, as well as representatives of that race. With *Carabus problematicus*, it is obvious that breeding operations cannot be undertaken. Besides, the problem is of a more complex nature than in other cases discussed. Nevertheless, up to the present, the picture emerging is not out of harmony with that outlined for the other insects dealt with above. However, a programme is being built in which it is proposed to bring under consideration its races from the northern Atlantic islands up to and including Iceland.

It will have been observed that, in reviewing the above species and the races, no mention has been made of clines. The failure to do so has been deliberate, and depends entirely upon the fact that field observations lend no support to the cline theory. Practically every scrap of evidence procurable supports the idea that we are concerned rather with zones of hybridization, occasionally irregularly distributed, developed by the interbreeding of Pleistocene stocks with others whose arrival in the British area can only be dated back to early Holocene times.

Take, for example, *Coenonympha tullia* treated so fully in Ford's *Butterflies* (pp. 292, 293; map 4, p. 342) as illustrating a cline. As far as Great Britain and the Scottish Western Isles are concerned, the map fails to give a correct distributional picture. The insects flying in the Cleveland District of Yorkshire, as well as those encountered in Northumberland, are not true *philoxenus* forms. Indeed, I have individuals in my series from Glaisdale indistinguishable from others taken in Kincardine. Moreover, amongst my Coll captures are some assignable to what Ford considers genuine *tullia*. Again, internal evidence exists in the book proving that that worker realized that the position was not truly that of a cline. In dealing with Islay populations, he is compelled to admit that they include specimens of *scotica*, *tullia* and "even specimens closely approaching *philoxenus*." One cannot wonder, therefore, that he has to write "The population must have evolved on somewhat independent lines." Finally, he attaches too little importance to the distribution of *Philoxenus* on the Continent for it suggests a very recent (probably boreal) advent of that race in Britain.

In conclusion, attention should be directed to the fact that the work outlined above is still in progress and that other reports will appear in future.

VESTRIAS PURPUREUS, THNB., AND ITS PREY.

By Dr G. H. Lowe.

This bug preys upon an ant of the genus *Monomorium* closely allied, if not identical, to **Monomorium pharaonis*, L. This ant is very common in Malaya, living in houses. I have never found it in any

*The ant is *Monomorium pharaonis*, L., only the specimens are very pale in colour.—H. D.